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The study of mate choice

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There are compelling reasons for believing that animals should not mate indiscriminately, but should choose their mates. Since individuals vary in their quality as potential mates, we would expect natural selection to have favoured mechanisms that ensure that mating occurs with partners of the highest possible quality. The word 'quality' is used here to cover a wide variety of properties of individual animals, including resources that they actually or potentially hold, their abilities as parents, and their genotype. Another reason why mate choice is a topic of considerable interest is that it is the behavioural mechanism that is central to the theory of intersexual selection as first propounded by Darwin (1871) and elaborated subsequently by Fisher (1930) and others (Halliday 1978*b*; Arnold, this volume, O'Donald, this volume).

The inherent plausibility of the hypothesis that mate choice is a common feature of the sexual behaviour of animals should make us especially cautious and critical in our evaluation of attempts to demonstrate its occurrence in nature. There is a danger that we may accept evidence of a standard that we would reject if it was presented in support of a more contentious hypothesis, for example, that birds use olfaction in orientation.

The principal aim of this chapter is to review some of the evidence for mate choice in animals and to discuss a number of conceptual and methodological problems that arise from studies of mate choice. A particularly important issue is the relationship between mate choice and mating competition which, since Darwin (1871) differentiated between inter- and intra-sexual selection, have typically been discussed as distinct and mutually exclusive processes. First, it is necessary to define what is meant by mate choice.

The definition of mate choice

Mate choice may be operationally defined as any pattern of behaviour, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than with others. It is important to note that this definition is in terms of observable behaviour and contains no reference to concepts that relate to the internal state of an animal, such as 'preference', as used in everyday language. The definition covers a variety of phenomena, some of which, in a human context, we would generally not call choice. For example, Ryan (1980) has shown that males of the frog *Physalaemus pustulosus* are more successful in attracting females if they produce complex calls consisting of a basic 'whine' followed by one or more 'chucks', than if they produce simple calls consisting only of a whine. Evidence that this does not represent a preference, in the usual sense of the word, on the part of females for complex calls, but is due to the fact that complex calls are more easily located, is provided by the observation that certain predatory bats, who use the males' calls to locate their prey, are more likely to take those males that produce complex calls (Ryan, Tuttle & Taft, 1981).

This example raises a difficult issue. What we may observe, at a behavioural level, is selective responsiveness by animals to particular stimuli. The mechanism by which the nervous system brings about such selectivity may involve sensory processing at the sense organ level, matching against a centrally-located template, or a preference developed through learning. However, for the purposes of understanding the dynamics of mating systems, the precise mechanism involved is irrelevant.

What is important in terms of the possible evolutionary consequences of mate choice is not whether a true preference is involved, but whether variations in the behaviour of members of one sex are correlated with variations in their mating success. The production of more complex calls by male *Physalaemus pustulosus* will be favoured by sexual selection, because they are more easily located by females, just as surely as they would be if females preferred them.

The benefits and criteria on which mate choice is based

There are many different kinds of benefit that animals may derive by choosing certain mates rather than others; these benefits may be realised more or less immediately. When choosing a mate, an animal may use as its criterion of mate quality, either the benefit itself, or some feature of the behaviour or appearance of prospective mates that is a predictor of the benefits that they offer.

Choice for high fecundity or fertility

In many animals, though less dramatically so in most birds and mammals, females continue to grow after reaching sexual maturity and become capable of producing larger numbers of progeny, or more viable progeny, as their body size increases. Male choice for larger, more fecund females has been described for the isopod *Asellus aquaticus* (Manning, 1975), the mormon cricket (*Anabrus simplex*) (Gwynne, 1981), and the mottled sculpin (*Cottus bairdi*) (Downhower & Brown, 1981). Males of the checkered white butterfly (*Pieris protodice*) exhibit choice on two criteria, preferring larger females and those that are young and, therefore, more likely to be virgins (Rutowski, 1982).

Female choice for males with high fertility may operate quite simply by females responding selectively to those males that court them most vigorously, provided that a male's display rate is correlated with his sperm supply (Halliday, 1978b). Such a correlation has been shown for smooth newts (*Triturus vulgaris*) (Halliday, 1976, 1978a) and for checkered white butterflies (Rutowski, 1979). Female newts, having responded positively to a male's display, also favour the most fertile males by being more likely to pick up each successive spermatophore that a male deposits (see below). In *Drosophila melanogaster*, yellow mutant males show lower courtship rates than normal males and, as a result, have reduced success in fertilising normal females (Bastock, 1956).

Choice for immediate gains and parental abilities

In a variety of species, males give females a gift of food as a necessary prelude to mating. Courtship feeding has been studied in the hanging fly, *Hylobittacus apicalis*, by Thornhill (1976, 1980). Females tend to accept only those males carrying insect prey larger than a certain size. Thornhill suggests that females may benefit from such a preference in three possible ways. First, since large insects take longer to eat and since the male mates while the female eats, large meals lead to longer copulations which, in turn, lead to accelerated oviposition. Secondly, the more food females get from males, the less they have to find for themselves and the lower the risk they run of being caught in a spider's web when searching for food. Thirdly, Thornhill has argued that males that bring large prey to females may be genetically of higher quality. However, the first two, immediate benefits are so substantial that the third, rather tenuous hypothesis seems to be redundant.

Among birds, food given to the female by the male during courtship may make an important contribution to her reproductive success, although it

may fulfil other functions, such as strengthening of the pair bond and appeasement of the female (Smith, 1980). Nisbet (1977) has shown that food provided during courtship feeding by male common terns (*Sterna hirundo*) contributes to a female's fecundity, and there is some evidence that females do not associate for long with males who feed them at a low rate (Nisbet, 1973). In the red-billed gull (*Larus novaehollandiae scopulinus*), females who are well fed by their males during one breeding season tend to remain with them in the next, whereas those which are inadequately fed seek new mates (Tasker & Mills, 1981).

In species in which males carry out some or all of the parental care of the young, females may choose males on the basis of their capacity to do so. Female mottled sculpins prefer larger males, who are more effective egg guardians, partly because they are less often absent from their nest than small males (Brown, 1981). Ridley & Rechten (1981) have shown that female sticklebacks (*Gasterosteus aculeatus*) are more likely to lay their eggs in male nests that already contain eggs than in empty nests. One of the advantages of this preference may be a simple dilution effect; the more eggs there are in a nest, the lower the chance that any one batch will be eaten by a conspecific or heterospecific predator. Another possible advantage relates to the fact that males keep other fish away from their nests more assiduously during the parental phase than during the courtship phase. Females who lay their eggs in full nests are more likely to be mating with a male who will soon enter the parental phase. Nisbet (1973) presents evidence that female common terns (*Sterna hirundo*) choose their mates on the basis of the quantity of fish brought to them by males during courtship feeding, using this as a predictor of their performance when later they feed the young. A male's courtship feeding performance is positively correlated with the total weight of the clutch that he subsequently fathers and cares for. Petrie (this volume) suggests that female moorhen (*Gallinula chloropus*) choose small fat males, who make the most effective incubators of eggs.

Choice for resources and for high male status

Where one sex holds resources that make an important contribution to the reproductive success of a mating pair, individuals of the other sex are expected to show preferences based on the quality of the resources held by prospective mates (Davies, 1978). Females of the wrasse, *Pseudolabrus celidotus*, show a tendency to choose males with territories in deeper water, where their eggs are most safe from predators (Jones, 1981). Female green frogs (*Rana clamitans*) choose those male territories that contain

dense vegetation in which to lay their eggs (Wells, 1977). Female bullfrogs (*Rana catesbeiana*) choose those males that hold territories whose water temperature ensures an optimum rate of egg development and in which predatory leeches are scarce (Howard, 1978). Female lark buntings (*Calamospiza melanocorys*) choose males holding territories in which there is good cover, ensuring that their eggs will be shaded from the sun (Pleszczynska, 1978). In the polygamous long-billed marsh wren (*Telmato-dytes palustris*), the number of females that a male attracts is influenced by the amount of food available in his territory (Verner & Engelsens, 1970). Lenington (1980) reports that female red-winged blackbirds (*Agelaius phoeniceus*) choose males holding territories on which the number of young fledged per nest is highest. However, predation rates on preferred territories are such that females choosing them do not have the highest reproductive success.

In species in which males establish dominance relationships with one another, it may be to a female's benefit to mate preferentially with a male of high status. The advantage she gains may be immediate, in terms of being able to mate without interruption by other males, or longer-term, if her progeny benefit from their father's high status through greater paternal care and protection. There may also be a genetic advantage, provided that an animal's ability to assume high status has some genetic basis.

In cockroaches (*Nauphoeta cinerea*), dominant males mate more often than expected on a random basis than subordinate males (Breed, Smith & Gall, 1980). This is partly due to the fact that dominant males are more active, and therefore encounter females more frequently, but is also attributable to females being able to discriminate between dominant and subordinate males on the basis of their odour.

Among primates, there is considerable variation, within and between species, in the extent to which high-ranking males obtain a majority of matings (Bernstein, 1976). One reason why dominant males may obtain fewer matings than expected is that females may develop preferences for particular, sub-dominant individuals (e.g. Packer, 1979). The importance of male dominance as a determinant of reproductive success in primates has probably been overemphasised (Hausfater, 1975). Bernstein (1976) suggests that what may be important in many primates is not the immediate choice that a female makes when she mates, but the establishment of long-term alliances between males and females which promote the survival of immature animals.

Choice for mate complementarity

The reproductive success of a mating pair may be affected not only by their various qualities as individuals, but also by the extent to which their genotypes and their capacities to expend reproductive effort, especially in parental care, complement one another.

An example of mate choice for genetic complementarity is provided by the assortative mating among ecotypes of the three-spined stickleback (*Gasterosteus aculeatus*) in Canada (Hay & McPhail, 1975). There are two forms; one is exclusively freshwater, the other is anadromous and lives mostly in the sea but returns to freshwater to breed. In choice experiments, 62% of females chose a male of their own type. Offspring of parents belonging to different ecotypes will be less well adapted to either habitat than pure-bred offspring.

Another aspect of genetic complementarity between mates is the degree of relatedness between them (Bateson, this volume; Partridge, this volume). Female chimpanzees tend to associate closely with their siblings until their first oestrus, when they abruptly start to avoid them (Pusey, 1980). At this time females commonly move to other groups, either permanently or temporarily, apparently attracted to unfamiliar males. Differential dispersal from their natal area by male and female birds tends to reduce the incidence of matings with close kin (Greenwood, Harvey & Perrins, 1978; Greenwood, 1980).

While it is generally argued that it will be adaptive for animals to avoid inbreeding, because of its harmful genetic consequences, some authors have suggested that it may be advantageous to mate with kin of a certain degree of relatedness (Bateson, 1980; Shields, 1983). While a cost of inbreeding is that it leads to a high level of homozygosity, and consequent expression of deleterious recessive alleles, a benefit is that it means that favourable gene combinations tend to be preserved. Bateson (1980) has argued for a mechanism ensuring an optimum level of breeding in Japanese Quail (*Coturnix coturnix*), which tend to avoid mating with very familiar individuals, who are likely to be siblings, but prefer birds similar to those with which they are reared to totally unfamiliar individuals. These preferred birds are likely to be kin with a coefficient of relatedness less than that of siblings (Bateson, 1982).

Complementarity in the reproductive behaviour of paired animals is especially important in species in which the pair bond is maintained over several breeding seasons. In Kittiwakes (*Rissa tridactyla*), pairs that stay together tend to show enhanced reproductive success as a result of their

accumulated breeding experience. However, if a newly-formed pair have low breeding success, they tend to split up and seek new mates (Coulson, 1966).

Choice for good physical condition

Whereas it may clearly be to the benefit of females to mate with males possessing 'good' genes, the criterion for such choice could never be the genes themselves, but would have to be some phenotypic expression of them. This expression might be in the form of general physical well-being (see Williams, this volume).

The question of whether animals can choose their mates on the basis of the quality of their genotypes is the most controversial issue in the mate choice literature. Two, very different problems are involved. The first concerns how animals might detect variations in the genetic quality of potential mates. The second is the more basic question of the heritability of fitness; to what extent are variations in fitness passed on to progeny? This second question is beyond the scope of this chapter but is discussed by Partridge elsewhere in this volume.

A point which I have alluded to in a number of the examples I have discussed earlier is that it is often not necessary to invoke a good gene argument to explain the adaptive value of mate choice. Where choice is directed towards short-term gains, such as resources, parental ability or fecundity, the benefits gained by animals that choose well may be so substantial that it is irrelevant whether or not the attributes chosen have a genetic basis that can be passed on to progeny.

Another important point is that mechanisms of mate choice will generally involve costs, as well as benefits. For a female to discriminate between males on the basis of their genotypes may be such a costly process, in terms of time spent or exposure to risks, that she may do better to choose a male at random. As discussed below, the pay-off from mating reliably with a member of the correct species may be much greater than that to be gained by discriminating between conspecifics (Gerhardt, 1982).

The handicap principle (Zahavi, 1975) proposes a mechanism by which females may detect the fitness of males. This theory has been much criticised (Maynard-Smith, 1976; Davis & O'Donald, 1976; Halliday, 1978*b*) and, if the handicap principle can work at all, it is probably only under certain, very limited conditions (Bell, 1978). A crucial point about the handicap principle is that it expressly discounts a basic function of male courtship displays, that they stimulate females, and that males will vary in their ability to attract females. If this effect is accepted, then it would

seem that the logic of Fisher's (1930) 'sexy son' hypothesis is irrefutable and the handicap argument becomes redundant.

In conclusion, the concept of mate choice for good genes is fraught with problems and must be regarded as an open question. Perhaps the only instances where it is tenable, on the basis of existing studies, are those where there is evidence that females choose older males, whose ability to survive may have a heritable basis.

Choice for the most effective courtship displays

If males vary in the vigour of their sexual displays, then, assuming that the effect of such displays is to increase female sexual motivation, females will be more likely to mate with the most vigorous males. Whether one chooses to interpret such an effect in terms of female choice or as a function of female motivation is a moot point, whose resolution depends on whether there is good reason to believe that the vigour of a male's display is a correlate of some measure of male quality, other than his fertility (see above). At present, there seems to be no convincing demonstration that this is so.

Given a choice of red and non-red males, female Three-spined Sticklebacks (*Gasterosteus aculeatus*) from Lake Wapato, Washington, show a significant preference for the rarer red form (Semler, 1971). This appears to be because red males are sexually more stimulating. However, the rarity of the red morph in this population (only 14% of males are red) suggests that it is at a severe selective disadvantage, probably through predation by trout. Male Pacific Treefrogs (*Hyla regilla*) form choruses which call in bouts, separated by silent periods (Whitney & Krebs, 1975). Females tend to pair with those males, called bout leaders, who call for longer, louder and at a faster rate than others in a chorus. Whitney & Krebs could find no convincing reason for believing that bout leaders are of higher quality than other males and suggest that, because they usually begin and end bouts of calling, and therefore call for some time on their own, they are easier for females to locate. Locatability of males has also been suggested as the basis of discrimination among males by female frogs (*Physalaemus pustulosus*), who are more likely to be attracted to males producing complex calls than to those producing simpler ones (Ryan, 1980).

Female choice for the most effective male displays provides the basis of Darwin's theory of intersexual selection, in which it is argued that selection will favour those characters that make males more attractive to females. Such characters, often referred to as epigamic characters, include such

morphological features as elaborate plumage and bright colours, as well as courtship displays. The evidence that females choose those males with the most highly developed epigamic characters is virtually non-existent, though Williams (this volume) has shown that female Mallard (*Anas platyrhynchos*) choose males with bright plumage. In fact, as discussed below, there is good reason to be sceptical about the role of female choice in the evolution of a number of male characters that are widely assumed to be epigamic.

Mate choice and mating competition

Darwin (1871) made a clear distinction between intrasexual selection, in which members of one sex compete directly with one another for mating opportunities, and intersexual selection, in which mating success depends on an individual's ability to attract members of the opposite sex. Whereas intrasexual selection has been widely accepted as the evolutionary process that has led to such male characters as large size, horns and antlers, intersexual selection has been the subject of considerable debate (Halliday, 1978*b*). The principal issue has been the concept that females may mate preferentially with certain males, simply because they find those males more attractive. Such apparently arbitrary, even whimsical, behaviour is in sharp contrast to the intensely utilitarian emphasis of the theory of natural selection. The question of what adaptive benefit females may gain by choosing certain males rather than others has been discussed above. In this section I wish to question the utility of the dichotomy between intrasexual and intersexual selection.

The mating rookeries of Elephant Seals (*Mirounga angustirostris*) have been described as an expression of 'rampant machismo'. Elephant seals provide one of the clearest examples of the behavioural basis and the evolutionary consequences of intense intrasexual selection. However, studies by Cox & Le Boeuf (1977) and Cox (1981) have shown that, despite the prevalence of male aggression, female elephant seals can exercise effective choice of mates. Females frequently protest when mounted by males, and are more likely to do so if a male attempting to mount them is of low status. The effect of a female's protests is to attract the attention of another male, who attacks the mounting male and makes it impossible for him to mate successfully. In effect, female elephant seals exercise choice in favour of high-status males. What this example shows is that intense competition among members of one sex does not preclude the expression of mate choice by the other sex.

It is also possible for mate choice and mating competition to be

important behaviour within the same sex. Although this possibility has not expressly been discounted, there is a temptation to regard female choice and inter-male competition as alternative processes leading to variation in male mating success. The degree to which both processes will occur in the same sex will depend largely on the extent to which members of one sex show a 'consensus' in terms of their choice of mates. A high level of consensus describes the situation in which all or most individuals of one sex choose the same individual, or a limited number of individuals, of the opposite sex. If it is not possible, or not adaptive, because of the dynamics of the particular mating system, for there to be a high level of polygamy, then members of the choosing sex may have to compete with one another in order to exercise their choice. Such behaviour may be called competitive mate choice (Altmann, Wagner & Lenington, 1977). In lek species, where male parental effort is limited to fertilising eggs, there may be little or no limit on an individual male's capacity to fertilise many females. Consequently, females will not incur significant costs if they all choose and mate with the same male. Conversely, in polygynous systems in which males hold important resources, a male's capacity to apportion parental effort to the offspring of a particular female will be reduced in proportion to the number of females that he acquires. Thus, we would expect females to compete with one another for exclusive access to the resources held by a male.

A number of studies provide evidence for competitive female choice. In Red-winged Blackbirds (*Agelaius phoeniceus*), those male territories most preferred by females, assessed in terms of the order in which females moved into them, do not contain the largest harems (Lenington, 1980). This appears to be due to resident females actively excluding those females that arrive later. Male Mormon Crickets (*Anabrus simplex*) produce large spermatophores that are rich in proteins (Gwynne, 1981). These proteins are eaten by females after mating and make an important contribution to females' reproductive effort. Females compete with one another for access to males, who call from elevated vegetation. Female Moorhens (*Gallinula chloropus*) frequently fight with one another, sometimes for males. The heaviest females tend to be most successful in fighting and also tend to pair with those males who are in the best condition, defined in terms of weight of fat reserves per unit body weight (Petrie, this volume). The small, fat males apparently chosen by females are probably the most effective at incubating eggs, a predominantly male activity, because of the reduced time that they will have to devote to foraging for food.

The conditions that favour competitive female choice may also make it possible for males to exercise mate choice. A female Mormon Cricket

who successfully competes for access to the plant stem on which a male is calling does not necessarily mate with him. Males reject all but the largest, most fecund females (Gwynne, 1981). Female Mottled Sculpins (*Cottus bairdi*) can increase their reproductive success significantly by mating preferentially with larger males, who are more effective guardians of eggs than small males (Brown, 1981). As a result of female choice for larger males, there is high variance in male mating success, with the largest males receiving as many as thirteen egg clumps. However, the advantage that a female gains by choosing a large male can be entirely lost if she is the last female to mate with him, since last egg masses have very low hatching success. The pressure to avoid spawning late has resulted in highly synchronised spawning among females (Downhower & Brown, 1981). This commonly results in more than one female approaching a male's burrow at the same time. In this situation, a male will generally court the largest, most fecund female rather than smaller ones.

The extent to which only one sex exercises mate choice, or whether both sexes choose, is likely to depend on the extent to which they make comparable investment in parental care. When both sexes make substantial parental investment, the reproductive success of each will depend on the quality of parental care performed by their partner. We would thus expect both partners to exercise choice. As the ratio of male to female parental investment departs from unity, mate choice should increasingly be more apparent in the behaviour of the higher-investing sex. This is a corollary of Trivers' (1972) principle that the intensity of competition within one sex depends on the extent to which it invests in parental care; mating competition should be most intense in the lower-investing sex.

What these examples show is that mate choice and mating competition are not alternative ways by which variance in mating success may come about. Within the mating system of a species, there may be competition among one sex and choice among the other, as in Elephant Seals, or choice and competition within the same sex, as in female Red-winged Blackbirds, Mormon Crickets and Moorhens, or both choice and competition may occur, to varying degrees, in both sexes, as in Mottled Sculpins.

That intrasexual and intersexual selection may be acting together in various ways within a single mating system does not invalidate Darwin's original dichotomy. These two concepts have considerable heuristic value in the analysis of the selection pressures that have produced sexually dimorphic characters. However, we should be extremely cautious about attributing any single character exclusively to one or other form of sexual selection. More important to the theme of this chapter, attempts to

demonstrate the occurrence of mate choice within a particular mating system may be made much more difficult by the simultaneous involvement of some form of mating competition.

Some classic epigamic characters revisited

Throughout the literature on evolution in general and on sexual selection in particular, it is commonplace for the results of intersexual selection to be exemplified by the peacock, birds of paradise and the ruff. The evidence that females actually choose their mates in these species is slight or non-existent. Indeed, some recent studies suggest that elaborate male plumage in these birds may be the evolutionary consequence of inter-male competition rather than female choice.

The mating system of birds of paradise has been investigated by Le Croy and co-workers (Le Croy, Kulupi & Peckover, 1980; Le Croy, 1981). In *Paradisaea decora*, only some males have elaborate plumes. Mating occurs in a small area, akin to a lek, consisting of a small group of tall trees. Each tree is occupied by two plumed males who are visited frequently by other plumed and unplumed males. The resident males display to one another, perform loud, duetting songs, and chase other males away. When the female visits a tree, the resident pair of males switch to performing silent displays to her. At this stage, any plumed males in the tree start to leave, though unplumed males remain. The display sequence reaches its peak when one of the resident pair of males moves aside, leaving his partner to display alone. The attending unplumed males then all copulate briefly with the female before the remaining plumed male starts a prolonged bout of copulation with her. Le Croy found no evidence that the identity of the males that females mated with was the result of any choice exerted by them. Within a tree, the same male performed all the final copulations that occurred, and was clearly dominant over his resident partner and over other males that visited the tree. The male dominance hierarchy is the result of display interactions between males that occur throughout the year.

These observations of the sexual behaviour of birds of paradise do not entirely preclude a role for female choice in the evolution of the males' elaborate plumage. Visual displays appear to be important in the sexual stimulation of the females, although male vocal displays are probably more important in the initial attraction of females to display trees. However, since the same display structures are used in interactions with other males, as well as with females, and since mating success seems to be determined primarily by male competition, it is most likely that the plumes of birds of paradise are more the result of intrasexual than of intersexual selection.

It may be a feature of many lekking species that male competition is more important than female choice in determining male mating success (but see Bradbury & Gibson, this volume). This will be true where female choice is directed towards males holding particular territories, usually central ones, and where possession of those territories is the product of male competition. There is evidence from studies of manakins (Lill, 1974), sage grouse (Wiley, 1973) and Uganda kob (Buechner & Schloeth, 1965) that females choose particular positions in leks rather than particular males. Leks typically occur in traditional sites, and it may be that, by choosing arbitrary positions, such as the centre, within a lek females force males to compete for those positions so that they can then mate selectively with the most competitive males (Davies, 1978).

For the European Ruff (*Philomachus pugnax*) interactions between males are a major factor in determining the distribution of matings among the males on a lek. Males of the dark morph establish territories by fighting and displaying to one another, but show varying degrees of tolerance to intrusions by the pale, non-aggressive satellite males (van Rhijn, 1973). The presence of satellites on a resident male's territory increases the number of females that visit him, but tends to reduce his copulation frequency. There is thus a trade-off between the costs and benefits of being tolerant to satellites and, when the rate of female visits is high, resident males tend to be more aggressive towards satellite males (van Rhijn, 1973). Shepard (1975) suggests that the mating choices shown by female ruff are based on some combination of three factors. Females exhibit choice for central territories, for males who display at a high rate, and for territories that contain satellite males. Only one of these factors, male display rate, directly involves female choice for a male characteristic. The other two, central position and presence of satellites, are products of inter-male competition.

Moyles & Boag (1981) have investigated how males establish territories within a lek in the Sharp-tailed Grouse (*Pedioecetus phasianellus*). Males are present at a lek for the greater part of the year and for much of that time no females are present. Male mortality is high and, as territories fall vacant, individual males tend to move centripetally into them. This process involves male displays and some fighting, and males in adult plumage have a competitive advantage over immature males. Clearly, direct competition between males is a major component of lekking behaviour.

In the Black Grouse (*Lyrurus tetrix*), females show a strong tendency to choose males holding central territories but, within the central group of territories, males who court in particularly attractive ways achieve high mating success (Kruijt & Hogan, 1967). The ability to adopt successful

courtship 'tactics' appears to be dependent on experience, and older males are more successful than younger ones.

The evolutionary pressures that brought about the peacock's tail are something of a mystery because no field studies have been made of peacocks (Ridley, 1981). However, Davison (1981) has studied a related, and equally striking species, the Argus Pheasant (*Argusianus argus*) in its forest habitat. Some males hold display sites which they largely clear of foliage; other adult and sub-adult males are non-territorial and move around widely. Davison found no evidence that females sample several males and exercise choice on the basis of their plumage, but suggests that they only mate with males that hold territories.

The tail of an argus pheasant takes several years to become fully developed. Its length and the number of ocelli on it are thus an indicator of a male's age (Davison, 1981). The same is true of male Lyrebirds (*Menura superba*), whose tails do not reach full development until they are seven or eight years old (Smith, 1965). In species in which a male's only contribution is his sperm, it can be argued that females will benefit by mating with older males, since they have a proven capacity to survive which, if it has a genetic basis, may be passed on to their progeny (Halliday, 1978*b*). The degree of development of male epigamic characters may, in species in which they take a long time to grow, be used by females as a means of identifying older males. This hypothesis is not incompatible with that which suggests that the better-developed adornments of older males are more effective at stimulating females (Ridley, 1981). However, the fact that, in argus pheasants, it is older, fully-plumed males who hold display territories suggests that male plumage development may be an important factor in competition between males.

Such field studies as have been carried out on species in which the evolution of elaborate male plumage has classically been attributed to female choice clearly cast doubt on that assumption. Not only is there no evidence that females sample several males in a way that intersexual selection theory would predict, but there is considerable evidence that the distribution of matings among males is largely determined by inter-male competition. Where female choice has been described, it plays an ancillary, and probably less significant, role than competition between males. Thus, the conclusion is the same as in the previous section; we must be very cautious about how the distinction between intrasexual and intersexual selection is used.

Modelling mate choice

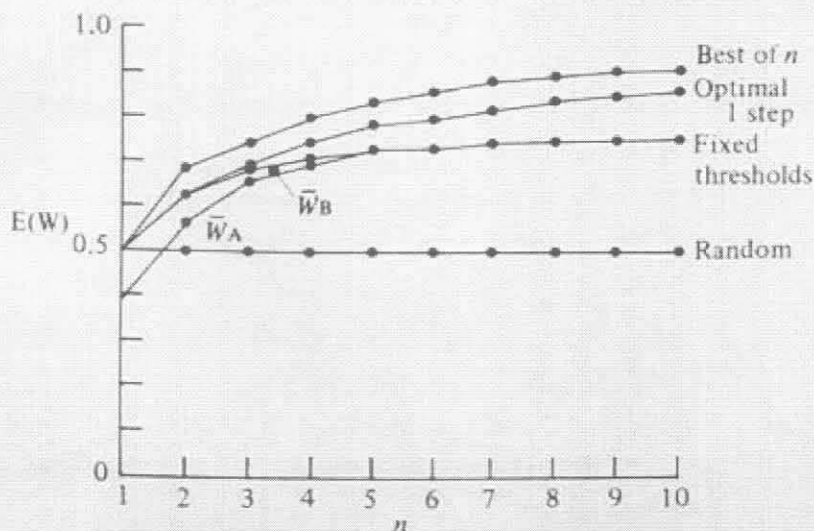
In setting out to investigate mate choice it may be helpful to detach oneself from the detailed analysis of how animals actually behave to consider how they might be expected to behave. This can be done by a modelling approach, in which one first defines the problems faced by an animal that has to choose a mate and then seeks the optimal solution to those problems. This kind of approach is discussed elsewhere in this volume by Wittenberger.

Janetos (1980) has developed a series of simple models of female choice. Among the female strategies that Janetos considers are:

- (i) Mating with a random male.
- (ii) Mating only with a male whose quality exceeds a pre-determined threshold value. A variant of this model allows a female to mate with a sub-threshold male if she has failed to meet one who exceeds her criterion within a certain time period.
- (iii) A one-step decision process, in which females initially have a high criterion which is gradually relaxed as they run out of time.
- (iv) Sampling n males and mating with the best of them. This is the only model in which females return to a male that they have met earlier.

Of these models, random mating yields the worst return to females, in terms of the fitness of their mates. The best of n males model gives the highest return, followed by the one-step decision model, followed by the fixed threshold model (Fig. 1.1). This is true whatever assumption is made about the shape of the male fitness distribution curve.

Fig. 1.1. The average expected fitness ($E(W)$) of males chosen by hypothetical females employing different choice strategies, as a function of n , the number of males sampled. From Janetos (1980).



The validity of the predictions of such models depends on the extent to which the models' assumptions are an accurate reflection of the natural situation. All the models assume that females mate only once, which is not true of many species, and that a male's fitness is not reduced as he accumulates matings, which will generally not be true in mating systems based on male defence of resources. It is also assumed that males are essentially passive, being randomly distributed in space and not interacting with one another in ways that influence their chances of mating. As emphasised earlier, mating competition is a widespread phenomenon which cannot be separated from mate choice in a simple way. Janetos counters this objection, not very convincingly, by asserting that female behaviour should be adapted to neutralise the effects of male competition.

Despite the fact that such assumptions are probably not appropriate to many natural situations, Janetos' approach has considerable value. As with many biological models, it forces one to be explicit about assumptions and mechanisms. For example, Janetos lists three constraints on a female's behaviour; time, mobility and memory. Time and mobility affect a female's ability to sample large numbers of males. The best of n model can only be effective if females accurately remember the characteristics of males they have sampled. This model, which yields the best results from a female's point of view, also requires that females have a lot of time and the opportunity to return to any male that they have sampled. Such conditions are probably rather rare in natural mating systems.

An important result that emerges from Janetos' study is that, as shown in Fig. 1.1, all models, except random mating, produce negatively accelerating curves as the number of males sampled by a female increases. In other words, the more males a female has sampled, the smaller is the expected pay-off from sampling one more male. Thus, whatever system of choice females employ, they need only sample a few males to ensure that they mate with a male whose fitness is well above average.

The value of Janetos' modelling approach is not that it provides models that can be directly applied to living species. Its assumptions are such that natural situations will, at best, only approximate to those envisaged in the models. What is of value is the emphasis on identifying constraints on female behaviour. In most mating systems, females are constrained in a variety of ways and, as a result, only certain kinds of choice will be open to them. However, these models suggest that very simple forms of female choice can yield large benefits to females, and that the ability to obtain good quality mates does not necessarily require females to have unrealistically high perceptual capacities.

Perhaps the most important conclusion to emerge from Janetos' models is that females obtain fitter mates if they assess on a relative, as opposed to an absolute, criterion. A relative criterion appears to be used by female mottled sculpins (*Cottus bairdi*) (Brown, 1981). The observed pairing behaviour of females fits very closely that predicted by a model in which each female samples a series of males and pairs with the first who is larger than the last one she met. The larger a male, the more effectively he defends eggs.

Demonstrating mate choice – some methodological problems

In this section I discuss a number of factors which may make the collection and interpretation of data on mate choice difficult. All the examples I use are of choice exercised by females.

(1) Mate choice may assume a very subtle form

In a majority of animals, males adopt the more active role in courtship and have a repertoire of ritualised, often very conspicuous displays. This makes the collection of data on male behaviour a relatively simple matter, and variations in male sexual responsiveness can usually be easily detected and quantified. By contrast, female courtship behaviour is often not in the form of stereotyped displays, but simply involves the adoption or non-adoption of receptive postures or movements. When a female is courted by more than one male at a time, she may exercise choice simply by moving towards a particular male. However, the observer may not be able to tell whether such a movement represents a positive female response, or whether she was moving in that direction for other reasons. This problem is very apparent in some species of lekking birds, where, as discussed earlier, the high mating success of certain males may be due, more to their topographical position within a lek than to any aspect of their behaviour directed towards females. A further complication is that, if a female approaches one of two males that are available to her, this may be wholly or partly due to behaviour shown towards her by that male, which may or may not be detected by the observer. This problem, as it relates to experimental studies of mate choice, is discussed by Bateson in this volume.

Variations in the behaviour of female Smooth Newts (*Triturus vulgaris*) may be interpreted as a very subtle form of mate choice. In newts, sperm is transferred by means of a spermatophore, and, in the course of a single courtship encounter, a male usually deposits a number of spermatophores on the substrate, each deposition being the culmination of a ritualised

courtship sequence (Halliday, 1974). The probability with which females pick spermatophores up increases with each successive sequence (Fig. 1.2). As a result, females are more likely to be inseminated by males who put down several spermatophores during a courtship encounter than by those who produce only one or two. These variations in female newt behaviour, which satisfy the definition of mate choice given earlier, are essentially a statistical effect which only becomes apparent when many observations of newt behaviour are analysed.

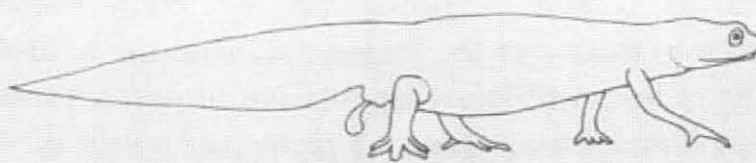
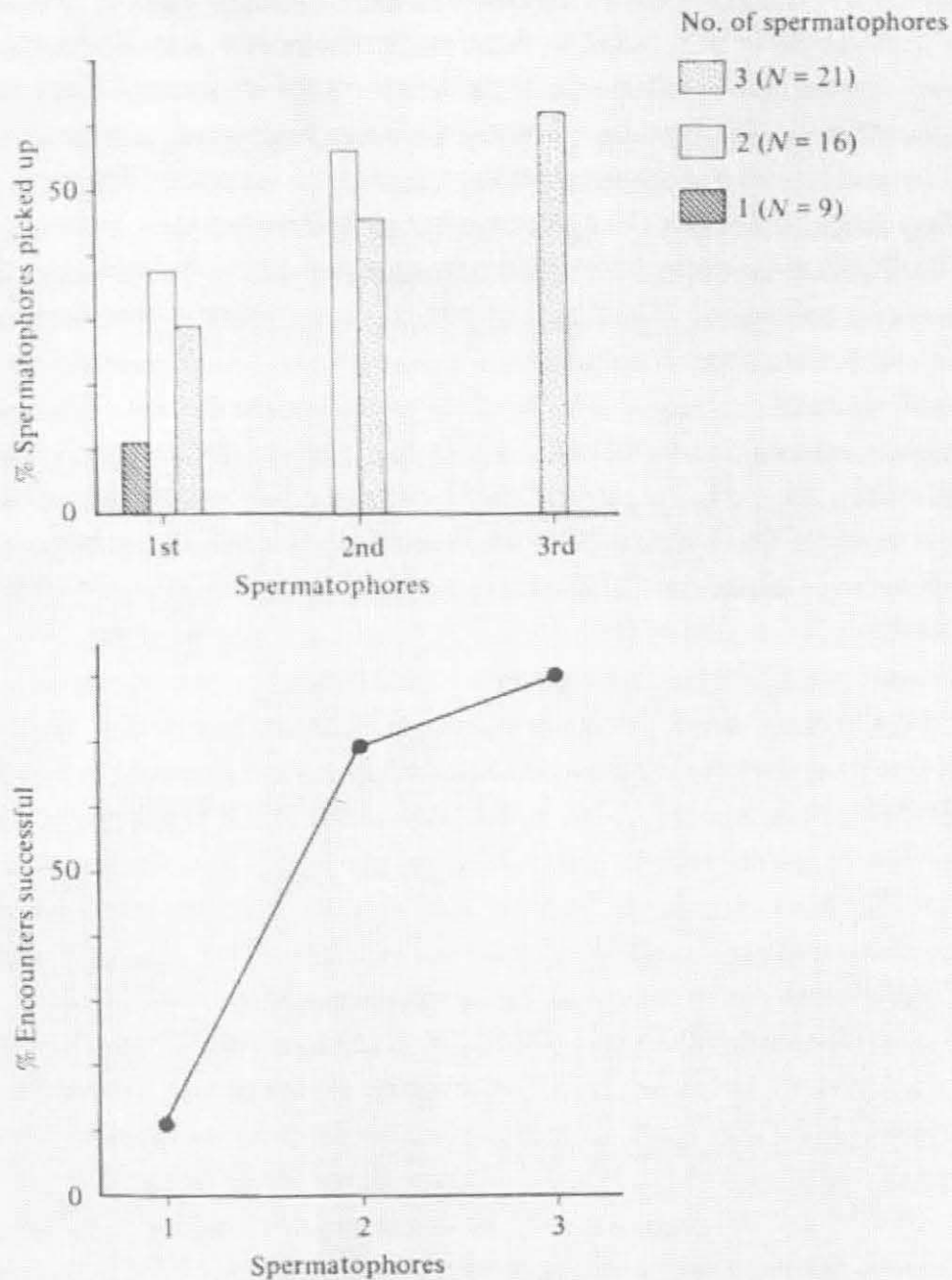
(2) *Mate choice may be masked by mating competition*

As discussed in previous sections, mate choice and mating competition may both be important determinants of the distribution of matings among individuals within a particular mating system. In elephant seals, fighting between males is spectacular and has such an obvious influence on male mating success, that the variations in female behaviour towards males of different rank, described by Cox & le Boeuf (1977) might easily have been overlooked. This, and other examples of the interaction between mate choice and mating competition were discussed in a previous section.

(3) *The scope for animals to choose mates may be constrained by other factors*

The Soldier Beetle (*Chauliognathus pennsylvanicus*) tends to aggregate on certain food plants, where mating also takes place. The same food plants are used by four species of wasp, which compete aggressively with the beetles for feeding space (McClain, 1981). When no wasps are present, female soldier beetles show a tendency to pair preferentially with larger males. However, on plants where wasps are present, females show no preferences and will even pair with males before their ova have fully developed. As a result, the proportion of beetles engaged in mating is higher on plants where there are also wasps than on those where they are absent. The explanation for this effect is that wasps are less aggressive to paired beetles than to single ones, so that female beetles are probably able to feed more efficiently when paired. Thus, in the presence of wasps, female Soldier Beetles becomes less punctilious in their choice of males and thereby benefit in terms of feeding efficiency. In this example, the extent to which mate choice can be demonstrated will depend on the ecological circumstances in which observations are made.

Fig. 1.2. Variation in female response to spermatophores in the Smooth Newt (*Triturus vulgaris*). Upper figure: the proportion of spermatophores picked up in relation to their order within a courtship encounter and to the total number deposited during an encounter. Lower figure: the proportion of encounters that are successful, i.e. at least one spermatophore is picked up, in relation to the number of spermatophores deposited during an encounter. Data from Halliday (1974).



(4) *Experiments on mate choice may be based on false assumptions*

The European Newts (*Triturus*) are unusual among tailed amphibians in being highly sexually dimorphic, males bearing bright colours and pronounced dorsal crests (Halliday, 1975, 1977). Since males show no kind of direct competition (with the possible exception of one species), it seems reasonable to assume that these male characters are the result of intersexual selection. However, the usual response of a female newt when simultaneously courted by two males is to swim vigorously away (P. A. Verrell, personal communication). They appear to avoid a situation in which they might compare the appearance of different males. Variations in female response to males seem to be entirely a matter of their response to spermatophores (Fig. 1.2), not to males' obvious physical characteristics, whose significance remains enigmatic.

Gerhardt (1982) has tested the responses of female Green Treefrogs (*Hyla cinerea*) to male calls of various frequencies. In this species, as in many anurans, the low frequency peak of a male's call is negatively correlated with his body size, so that larger males produce a lower-pitched sound. The range of values for the low frequency peak in *Hyla cinerea* is 700 to 1250 Hz. Using synthetic calls, Gerhardt tested the responses of females when given a choice between a call of 900 Hz, representing the middle of the species range, and calls of higher or lower frequency. In both two-way and four-way choice experiments, females showed a clear tendency to avoid calls near either the upper or the lower end of the frequency range in favour of those of intermediate frequency. *Hyla cinerea* frequently breeds in the same ponds as two closely related species, the Barking Treefrog (*Hyla gratiosa*) and the Squirrel Treefrog (*Hyla squirella*). The low frequency peak of the male call varies between 400 and 500 Hz in *Hyla gratiosa*, and between 1000 and 1400 Hz in *Hyla squirella*. Thus, the calls of these two species fall either side, and slightly overlap with the range of *Hyla cinerea* calls. Gerhardt interprets the preference of female Green Treefrogs for male calls in the middle of the species range as an adaptation that reduces the risk of engaging in hybrid mating with males of either of the other two species that share their breeding pond.

A number of authors (Licht, 1976; Davies & Halliday, 1977; Wilbur, Rubenstein & Fairchild, 1978) have suggested that, for many female anurans, it will be adaptive to mate with the largest available males, since these will tend to be the oldest, and therefore to have proven survival capabilities. However, for Green Treefrogs such a preference would carry

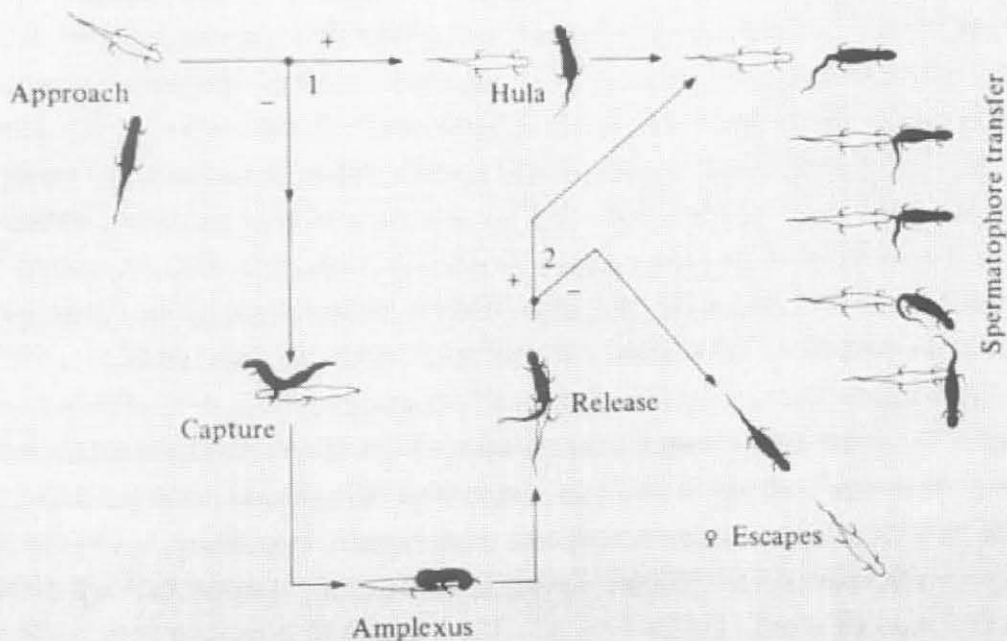
considerable risk of engaging in a hybrid mating. The gain that a female may derive by mating with a particular conspecific male who is of higher quality than another will be much smaller than the cost she will incur from a hybrid mating. Females appear to avoid actively those males who, on *a priori* grounds, appear to be the most desirable mates.

(5) *Mate choice may be masked or confounded by motivational effects*

The behavioural criterion that female choice has occurred will often be whether or not a female responds positively to a male's courtship behaviour. However, a female's responsiveness to males at any given moment is also a function of her sexual motivation. Thus, when a female fails to respond to a male, we can interpret this either as her rejecting him as a suitable mate, or as her having low sexual receptivity. Conversely, if a female responds positively to a male, this may not necessarily represent a positive choice from among several males, because she may be so strongly motivated that she is responding to the first male that displays to her. The following examples illustrate the complex interaction between female choice and sexual motivation.

The North American Red-spotted Newt (*Notophthalmus viridescens*) has alternative modes of courtship (Fig. 1.3) (Verrell, 1982). When a male first approaches a female, she commonly swims away; the male pursues

Fig. 1.3. Alternative forms of courtship in the Red-spotted Newt, *Notophthalmus viridescens*. The male is shown in black. Based on Verrell (1982).



her and attempts to clasp her round the neck with his hindlimbs. If he succeeds, there follows a prolonged period of amplexus, which may last for as long as three hours, during which he stimulates the female by rubbing glands on his cheeks against her snout and by beating his tail. Amplexus ends when the male releases the female and slips in front of her. If she is responsive, she follows him, and the male initiates spermatophore transfer behaviour; if she is unresponsive, she swims away. A much quicker sequence occurs when the female is initially responsive to the male. If she does not swim away when first approached, the male performs a 'hula' display, in which he waggles his body and tail. If she then approaches him, he turns and begins the spermatophore transfer phase. This quick courtship mode, in which there is no amplexus, takes only a few minutes. In both courtship modes, the male usually deposits several spermatophores during the spermatophore transfer phase.

There are at least two points in a sequence when a female may or may not respond positively to a male (see Fig. 1.3). Point 1 is when the male first approaches her, point 2 is when the male releases her at the end of amplexus. Point 2 is only reached if her response at point 1 was negative. A third point at which a female may be regarded as exercising some sort of choice is when she picks up, or fails to pick up a spermatophore, though red-spotted newts do not show the order effect shown by smooth newts, illustrated in Fig. 1.2 (Verrell, 1982).

The fact that most females (71%) who are unresponsive when first approached by a male have become responsive after capture and amplexus, suggests that the function of the male's cheek-rubbing and tail-beating during amplexus is to raise her sexual receptivity. The corollary of this is that females who do respond positively when first approached are so highly motivated that they require no stimulation from males. If females are exercising some kind of choice, those who are initially responsive must make only a minimal assessment of a male, whereas those who go through capture and amplexus appear to have ample opportunity to assess males on the basis of their courtship. Females who escape when released by the male at the end of amplexus have either rejected them as unsuitable mates, or have not been sufficiently stimulated by male courtship.

A curious feature of this dual pattern of courtship is that those females who respond immediately to males and go through the quick courtship sequence are less likely to be inseminated than those who go through the longer, amplexus sequence. Following quick courtship, only 26.2% of spermatophores are picked up, whereas 62.2% are picked up following amplexus (Verrell, 1982).

It is important to remember that courtship behaviour fulfils a variety

of functions, which Tinbergen (1953) summarised as orientation, persuasion, synchronisation and reproductive isolation. We should not allow our preoccupation with interpreting male courtship as a means by which females may assess males to lead us to ignore these other important functions. The word 'persuasion' refers to the role of displays by one partner, usually the male, in increasing the sexual motivation of the other partner. In some species, male displays play a vital role in bringing females into full reproductive condition. Female Green Anoles (*Anolis carolinensis*) will only complete their ovarian development, to the extent of producing shelled eggs, if they are exposed to sexually active males (Crews, 1980). For female Ring Doves (*Streptopelia risoria*), exposure to courting males is essential for secretion of oestrogen and progesterone to reach effective levels. Females exposed to castrated males show significantly reduced follicular size, oviduct weight and ovulation frequency, in comparison to those exposed to intact, sexually active males (Erickson & Lehrman, 1964; Erickson, 1970). In animals such as these, females may solicit courtship from several males but fail to respond positively to most of them. However, it would be misleading to infer that they have rejected them as suitable mates. Failure to respond to a male may more often be a function of a female's motivational state than of her assessment of males as suitable mating partners. While we may be able to interpret a positive female response in terms of choice for a certain male, we cannot make such an inference about negative responses.

In the pomacentrid fish *Chromis cyanea* females visit and are courted by territorial males (de Boer, 1981). It appears that when a female mates with a particular male, it is not the result of any critical aspect of his behaviour, but of the cumulative effect of all the male courtship that she has received. It seems that she must be subjected to a certain amount of courtship before she is ready to spawn. A few males, each displaying for a long time, have a comparable effect to many males, each displaying for a short time.

The same problem of interpretation arises in species in which the 'normal' sex roles are reversed and the female plays an active role in courtship. In the butterfly *Pieris protodice*, females frequently chase conspecific males and solicit matings (Rutowski, 1980). Female solicitation is shown most strongly by females who are virgins or who are carrying spermatophores that are significantly smaller than average. Thus when a female solicits a mating from a male, it appears that her behaviour is motivated by the need to maintain a good supply of sperm, not by a preference based on male quality.

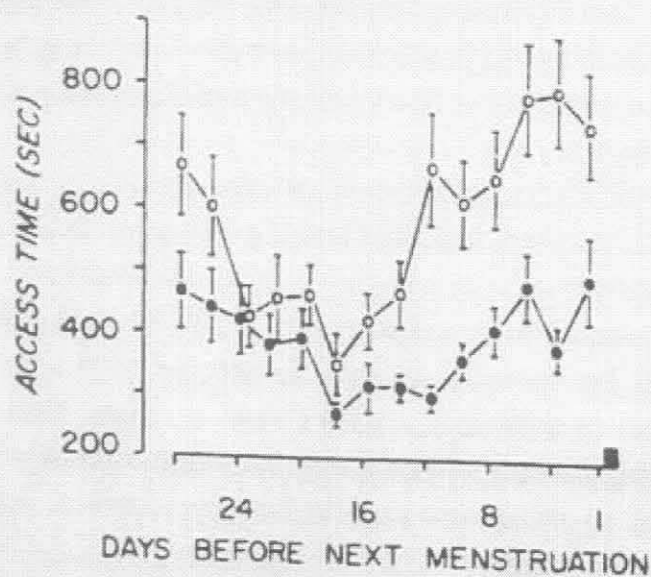
In a laboratory study of sexual behaviour in Rhesus Monkeys (*Macaca*

mulatta), Michael and co-workers have directly assessed the motivational state of females by means of an operant procedure (Michael & Bonsall, 1977). To gain access to a male, a female must press a lever 250 times. The time that she takes to do this is a measure of her sexual motivation and changes in a characteristic way over the course of the menstrual cycle (Fig. 1.4). Females gain access to males most quickly near mid-cycle, when ovulation occurs. Bonsall, Zumpe & Michael (1978) compared the behaviour of females working to gain access to males for whom they showed a preference, with their behaviour towards non-preferred males. Before and after the few days around ovulation, females worked considerably harder to reach preferred than non-preferred males, but this difference is less marked around ovulation (Fig. 1.4). Thus a female's preference for a particular male is much more apparent when her sexual motivation is relatively low than when it is very high.

A related complication is that females may express different choices at different times, according to their physiological state. Some days away from ovulation, a female baboon may consort with a subordinate male, but, at the time of ovulation, she may switch her attention to a dominant male (see Keverne, this volume).

All these examples illustrate that a female's motivational state and her expression of mate choice interact in a complex way. Consequently, we

Fig. 1.4. Changes in the sexual motivation of captive female Rhesus Monkeys in an experiment in which they had to press a bar 250 times to gain access to a male. Closed circles, responses to preferred males; open circles, responses to non-preferred males. (From Bonsall *et al.* (1978). Copyright (1978) by the American Psychological Association. Reprinted by permission of the authors.)



should be extremely cautious about interpreting individual positive or negative responses by females to males as expressions of mating choices. Such interpretations are only valid if we have a clear picture of the female's motivational state at the moment she makes each response.

(6) *Individuals may mate with several partners*

In some mating systems, females mate with several males, but this does not necessarily mean that they do not exercise some sort of mate choice. A female may ensure that a particular male fathers her progeny by mating exclusively with him at the point in her reproductive cycle when she is most likely to conceive, and by mating with non-preferred males at other times. Reviewing the literature on male dominance hierarchies and reproductive success in primate societies, Bernstein (1976) points out that the relationship between a male's rank and his reproductive success is often not as clear-cut as many authors have suggested. Hausfater (1975) found that, among wild baboons (*Papio cynocephalus*), high-ranking males achieved fewer, and low-ranking males more, copulations than expected on the basis of a simple priority-of-access model, which assumes that a male's ability to gain matings is solely determined by his rank. However, Hausfater's data do not permit analysis of which matings were successful in terms of conception. Such an analysis has been made in a study of captive Rhesus Monkeys by Duvall, Bernstein & Gordon (1976), who tested the paternity of offspring and found that male rank was rather a poor correlate of the distribution of successful matings. Packer (1979) has listed several factors that may lead to male mating success not being correlated with male status in olive baboons (*Papio anubis*); one of these is female choice. In many social primates, females may mate with several males, but it is quite possible that they choose the fathers of their progeny by consorting with certain males at critical times in their reproductive cycle.

The role of mate choice by females who mate with several males may be even more complex in species that show sperm competition. Sperm competition of the type described for insects by Parker (1970), in which ejaculates from different males compete for access to a female's eggs, is usually regarded as a form of inter-male competition. However, as Walker (1980) has pointed out, because the form that sperm competition takes depends on the anatomy, physiology and behaviour of females, it is important that we should consider it as an adaptive aspect of female reproductive biology. For example, it is possible that a female could use that form of sperm competition in which the last male's ejaculate has precedence over the ejaculates of previous males, to ensure that her eggs

are fertilised by a male of the highest possible quality, in the following way. If she mates with the first male she meets, she can guarantee that her eggs will be fertilised. Thereafter, she can sample further males and, by mating only with males of higher quality than the first, she can maximise the quality of her progeny. Such a mechanism is entirely speculative, but it demonstrates that multiple mating by females need not imply that they do not exercise mate choice.

If females do engage in several matings, then the only reliable evidence that mate choice has occurred is that obtained by testing the paternity of their offspring. At present, data on paternity are very scarce, but, in the future, such studies may be of great importance in providing conclusive evidence for mate choice.

Summary

That animals choose their mates, as opposed to mating indiscriminately, is an attractive and evolutionarily important hypothesis. There are many different kinds of benefit that animals may derive by choosing a particular mate, ranging from the immediate gain provided by courtship feeding to the long-term advantage of mating with an individual of high genetic quality. There is abundant evidence for mate choice that yields short-term benefits, such as resources that support breeding effort. However, the evidence for long-term benefits relating to the genotype of a chosen mate is very weak, and this is an area that requires considerable theoretical and empirical investigation.

Mate choice is only one of many factors that may determine the distribution of matings among individuals in a breeding population. Most important of these is mating competition. There are strong theoretical reasons for supposing that mate choice and mating competition will often occur together and interact within a single mating system, and this view is confirmed by a number of studies.

The long-accepted role of female choice in the evolution of male epigamic characters is challenged by recent studies of certain sexually-dimorphic species, notably birds of paradise and lekking species. These studies suggest that competition between males is a more potent force in these species than female choice.

A number of methodological problems involved in the collection and interpretation of data on mate choice are discussed. Among these is the fact that other processes, notably mating competition, are at work in many mating systems. A general conclusion is that, in seeking to demonstrate mate choice, we may overlook other important biological functions of

sexual behaviour, such as the role of displays in stimulating males, and in ensuring reproductive isolation. A modelling approach may facilitate the investigation of mate choice by encouraging the comparison of alternative hypotheses and a greater rigour in the formulation of assumptions about behavioural mechanisms.

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